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BLACK-THROATED BLUE WARBLER AND VEERY ABUNDANCE IN RELATION TO UNDERSTORY COMPOSITION IN NORTHERN MICHIGAN FORESTS

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ABSTRACT.—Balsam fir (*Abies balsamea*) understory may be an important predictor of Black-throated Blue Warbler (*Dendroica caerulescens*) and Veery (*Catharus fuscescens*) distributions in northern hardwood forests that are heavily browsed by white-tailed deer (*Odocoileus virginianus*). We examined the abundance and age ratios of Black-throated Blue Warblers, and the abundance of Veerys, in 16 plots of hardwood forest with different understory composition within a heavily browsed region of the Hiawatha National Forest in Michigan's eastern Upper Peninsula. Four of these 36-ha plots had minimal understory and 12 had dense understory with variable amounts of balsam fir. Black-throated Blue Warbler abundance was significantly greater in plots with an average of 27% balsam fir understory cover than in plots dominated by deciduous understory; no Black-throated Blue Warblers were detected on the minimal understory plots. Age ratios did not differ significantly relative to balsam fir understory density. Veery abundance also did not vary with balsam fir understory density, but it increased with overall understory density. In forests such as these, where deer are abundant but rarely browse balsam fir, active management of balsam fir understory could provide key habitat for sustaining populations of Black-throated Blue Warblers and Veerys. We recommend that managers consider the presence of balsam firs in the understory when planning forest harvests in deer-impacted areas, so that they leave some balsam fir and stagger the cutting of stands with balsam fir over time to create and maintain heterogeneous understory structure. *Received 2 September 2005, accepted 16 May 2006.*

Identifying key habitat characteristics that predict songbird distributions represents an important step towards incorporating songbirds into forest management plans (Martin 1992, Donovan et al. 2002). In the eastern United States, browsing of understory vegetation by white-tailed deer (*Odocoileus virginianus*) produces forests that differ in terms of their structural characteristics and plant species compositions from those in less impacted areas (reviewed by Rooney and Waller 2003, Côté et al. 2004), and these changes can affect the abundance of understory-dependent songbirds (Casey and Hein 1983, deCalesta 1994, McShea and Rappole 2000). Browsing impacts, however, are likely to differ across species' ranges because of variation in the plant community, the landscape context, and, in the Great Lakes region, the degree to which the understory is protected from deer by snow. Therefore, predicting the abundance of understory-dependent birds is best approached using habitat indicators based on local information, a key element of which may be the distribution of browse-resistant plants.

We investigated the relationship between understory characteristics and the abundance of two forest songbird species, the Black-throated Blue Warbler (*Dendroica caerulescens*; BTBW) and the Veery (*Catharus fuscescens*), in managed northern hardwood forests in the eastern Upper Peninsula of Michigan, where the overabundance of deer is a conservation concern (The Nature Conservancy 2000, Rooney and Waller 2003, Kraft et al. 2004). Our sites were dominated by sugar maple (*Acer saccharum*) and located near coniferous forest "deeryards"—areas that provide winter habitat for high densities of deer (Van Deelen et al. 1998). At similar Great Lakes forest sites, browsing has decreased understory density and reduced structural complexity, especially for sugar maple seedlings and saplings (Alverson et al. 1988, Kraft et al. 2004).

Veerys and BTBWs are likely to be susceptible to browsing impacts because they nest and forage in the understory (Holmes 1994, Moskoff 1995). Both species are also of con-

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servation concern in northern forests (U.S. Fish and Wildlife Service 2002; Matteson et al. in press). BTBWs have been studied intensively in New Hampshire, where population density is positively associated with shrub and sapling density (Steele 1992, 1993; Holmes et al. 1996), and the density of deciduous leaves in the shrub layer is a key predictor of territory quality (Rodenhouse et al. 2003). Less is known about key habitat features for Veerys but, in Michigan, they are typically found in mesic to wet forest with dense understory and a conifer component (Winnett-Murray 1991).

We hypothesized that the density of understory balsam fir (*Abies balsamea*), a species rarely browsed by deer in our region (Borgmann et al. 1999), may better predict BTBW abundance than deciduous species in Great Lakes forests. Our previous work in Michigan hardwood forests near deeryards revealed that 100-m-radius point-count locations with abundant balsam fir had higher relative abundances of BTBWs than locations with dense, deciduous-dominated understory (Hall 2002). In this paper, we considered a management-relevant scale (36-ha stand) and compared BTBW and Veery abundance between plots that varied in their proportion of balsam fir understory. We also predicted that areas with more balsam fir would have a higher ratio of older to yearling BTBWs, thus indicating habitat preference (Holmes et al. 1996, Hunt 1996).

METHODS

Study area.—We collected data in 16 stands of mature, relatively even-aged hardwood forest within a section ($\sim 15 \times 7$ km^2) of the southeastern Hiawatha National Forest in Mackinac County, Michigan, between 46° 09′ 06″ N to 46° 05′ 18″ N and 84° 52′ 23″ W to 84° 40′ 50″ W (Fig. 1). All plots were located within the St. Ignace subsection of the Niagaran Escarpment, an area characterized by shallow morainal soils and occasional glacial erratics (Albert 1995). Sugar maple was the dominant overstory tree on the study plots, but often was co-dominant with American beech (*Fagus grandifolia*) and, to a lesser extent, aspen (*Populus* spp.), paper birch (*Betula papyrifera*), and American basswood (*Tilia americana*); rarely, balsam fir and white pine (*Pinus strobus*) were also co-dominant. Typical understory species included sugar maple, hop-hornbeam (*Ostrya virginiana*), and balsam fir; occasionally we found seedlings and saplings of other canopy species and white spruce (*Picea glauca*), white ash (*Fraxinus americana*), and black cherry (*Prunus serotina*). The study area receives an annual average of 1.5–2 m of snow (Albert 1995), which appears to protect many plants from being completely removed by overwintering deer that seek shelter in the nearby deeryards and enter these stands to forage.

We chose site locations using a 2002 GIS database of forest management units in the Hiawatha National Forest within the Niagaran Escarpment (U.S. Department of Agriculture Forest Service unpubl. data). We used ArcView (Environmental Systems Research Institute 2002) to select hardwood management units large enough to accommodate a square 36-ha plot, then visited those units in random order for the purpose of selecting our 16 sites, with four in each of the following understory categories: (1) minimal understory vegetation, (2) deciduous-dominated understory vegetation with sparse balsam fir, (3) understory vegetation with moderate balsam fir density, and (4) understory vegetation with high balsam fir density (Fig. 1). The initial assignment of sites to understory categories was based on visual estimates conducted in May, prior to the standardized collection of vegetation data (see below). The dark vegetated areas (Fig. 1) were dominated by coniferous overstory and comprised the habitat type typical of deeryards in this region (Van Deelen et al. 1998). The 36-ha plot size was small enough so that sites were internally similar (e.g., within the same management unit, with similar canopy cover and understory density, and with few old logging roads or other openings), yet large enough to encompass a wide range in the number of BTBW territories (typically 1–4 ha in size; Holmes 1994, Hall 2002).

Vegetation sampling.—We measured understory composition using a modified method from Mueller-Dombois and Ellenberg (1974). Within each plot, we established three parallel, 600-m transects spaced 200 m apart, and randomly oriented the transects east-west or north-south. We then divided each transect into 100-m segments and randomly chose a 16-m^2 quadrat within each segment, for a total

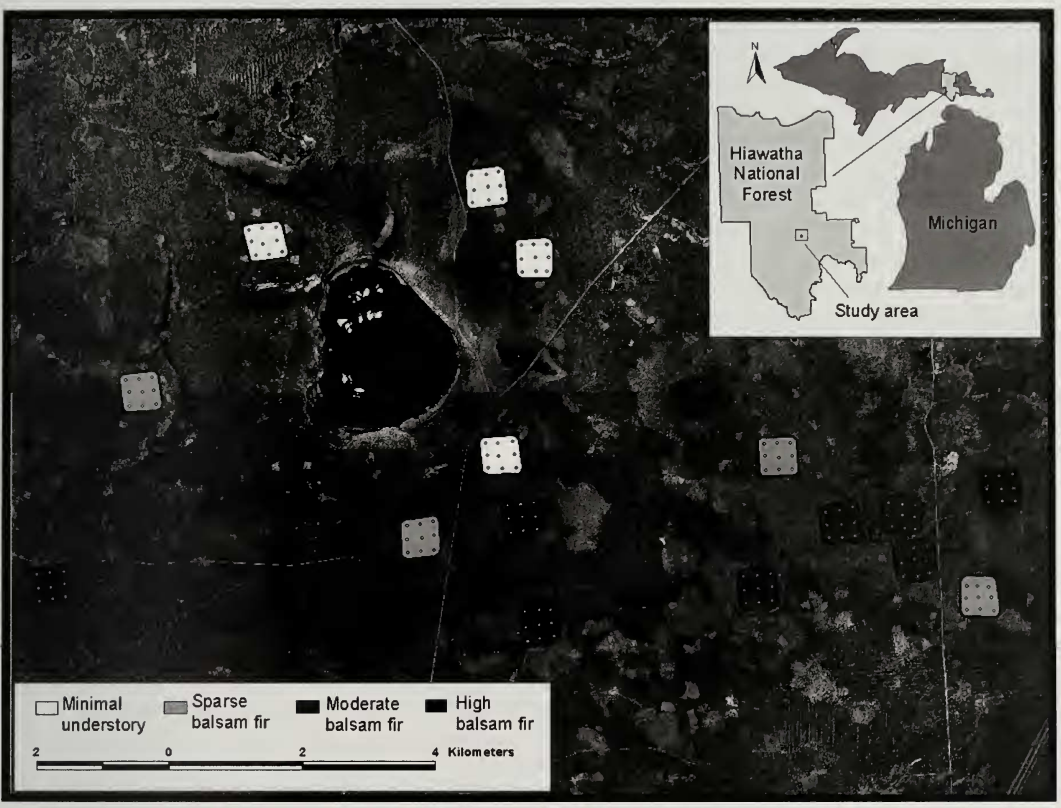

FIG. 1. Distribution of four understory vegetation plot types in the Hiawatha National Forest, Mackinac County, Michigan, summers 2002 and 2003. Digital orthophoto taken before leaf-out in March 2001 shows conifer stands in dark gray, hardwood stands in light gray, and water in near black. Squares represent 36-ha plots (n = 16): white = minimal understory, light gray = deciduous-dominated understory with sparse stem densities of balsam fir, dark gray = understory with moderate balsam fir density, black = understory with high balsam fir density. Points in each plot (n = 9) represent approximate locations of 100-m radius avian point counts and 11.3-m overstory sampling subplots. (Sources: Environmental Systems Research Institute 2002 Projection: UTM Zone 16 N, Datum: NAD 1927; U.S. Department of Agriculture Forest Service unpubl. data.)

of 18 quadrats per plot. For each quadrat, we calculated the total stem count and average percent cover of woody understory plant species within six height categories—five 0.5-m categories (ranging from 0.5 to 3 m) and a 3- to 5-m category—based on estimates from four 4-m^2 sub-quadrats. Using a spherical densiometer, we also measured the canopy cover in each quadrat. Following a modification of James and Shugart's (1970) vegetation sampling method, in each 36-ha plot we established nine points spaced 200 m apart on a 3 × 3 grid (Fig. 1); within an 11.3-m radius of each point, we counted the number of trees in two size categories (small: 7.5–22.5 cm in diameter at breast height [dbh], large: ≥22.5 cm dbh). We sampled all vegetation between late July and September, prior to leaf fall, in 2002 and 2003.

We calculated mean stem density, percent cover, and height for both balsam fir and deciduous understory species from the 18 quadrats in each plot. We calculated the standard deviation of percent cover as a measure of understory patchiness. We used the standard deviation of height as a measure of understory vertical structure. We also determined mean density of small and large trees in the 11.3-m point samples.

Bird sampling.—In 2002, we measured the abundance of territorial male BTBWs by target-netting and color-banding birds. An observer (LJK) first surveyed each plot during late May–early June by walking the three transects and using song playbacks to detect and record the locations of BTBWs; Wolf et al. (1995) estimated that BTBW song is detectable up to 120 m from an observer. Plots were revisited up to 10 more times between late May and late July, depending on the density of male BTBWs and how catchable they were. During these visits, two or three observers once again searched the plots for male BTBWs by walking transects and using song playbacks; nearly all males within each plot were captured and color-banded by targeted mist-netting (song playback and model bird). We banded each bird with a federal aluminum leg band and two colored plastic leg bands. During banding, we determined age as older (after second year; ASY) or yearling (second year; SY) on the basis of plumage characteristics (Pyle 1997). Experienced observers (KRH, LJK) aged three uncatchable birds by using binoculars to study their plumage characteristics (Graves 1997a). Between late May and early June 2003, we systematically resurveyed all plots using song playback to determine 2003 abundance.

From early June to mid-July 2002, we conducted 10-min point counts (100-m fixed radius) of singing males to estimate the relative abundances of Veerys and BTBWs (as a second measure) in each plot (Ralph et al. 1993). For each bird, we recorded its location within one of three distance categories (0–25, 25–50, 50–100 m) and time to detection (0–3, 3–5, 5–10 min). Weather permitting, LJK surveyed one plot per day, starting the count within 30 min of sunrise. After randomly selecting a starting point from one of the nine points within a given plot (Fig. 1), the observer conducted the count following the most efficient route. We minimized the potential for double-counting birds that moved between survey points by eliminating individual detections in similar locations on adjacent counts. Since BTBWs often move quickly across large territories (e.g., >200 m in diameter; Hall 2002), double-counting birds during point counts was a particular concern. Thus, our BTBW analyses focused on the banding data, whereas we used the point count data only as an additional measure of BTBW abundance and to verify that we had banded all birds in locations where they were detected during point counts.

Statistical analyses.—We performed Principle Components Analysis (PCA) using the correlation matrix for 13 vegetation variables to explore the relationship between vegetation characteristics in the 16 plots and to evaluate our visual estimates of plot characteristics. We investigated the relationships of BTBW abundance and age ratio (percent older birds), and Veery abundance, to plot characteristics by comparing the bird variables among plot types (Kruskal-Wallis test, $\alpha = 0.05$; Zar 1999) and by correlating abundance with plot scores for principal components with eigenvalues >1. Statistical analyses were conducted in S-Plus 6.1 (Insightful Corporation 2002). Means are presented ± SE.

TABLE 1. Eigenvectors of the first three principal components for 13 vegetation variables measured in 36-ha plots ($n = 16$) in the Hiawatha National Forest, Michigan, summer 2002. The standard deviation (SD) of percent cover for the 18 16-m^2 quadrats in each plot was a measure of vegetation patchiness; the SD of average height was a measure of vertical structure.

Variable	Eigenvectors		
	PCA1	PCA2	PCA3
Canopy cover	−0.14	−0.32	−0.07
Large-tree density	−0.30	−0.33	0.20
Small-tree density	0.36	0.06	−0.02
Balsam fir			
Stem density	0.37	0.03	−0.04
Percent cover	0.38	0.03	0.01
Cover SD	0.37	0.06	−0.14
Height	0.31	0.09	−0.00
Height SD	0.36	0.11	−0.01
Deciduous spp.			
Stem density	−0.19	0.44	−0.10
Percent cover	−0.21	0.51	−0.10
Cover SD	−0.21	0.47	0.04
Height	0.02	0.24	0.61
Height SD	0.04	0.16	0.65

RESULTS

Vegetation.—Principle components analysis identified three axes that accounted for 84% of the variation in vegetation measurements. The first principle component, which accounted for 50% of the variation (eigenvalue = 6.5), positively weighted all balsam fir variables and small-tree density, and negatively weighted deciduous understory and large-tree density (Table 1). This component distinguished the eight plots classified by visual es-

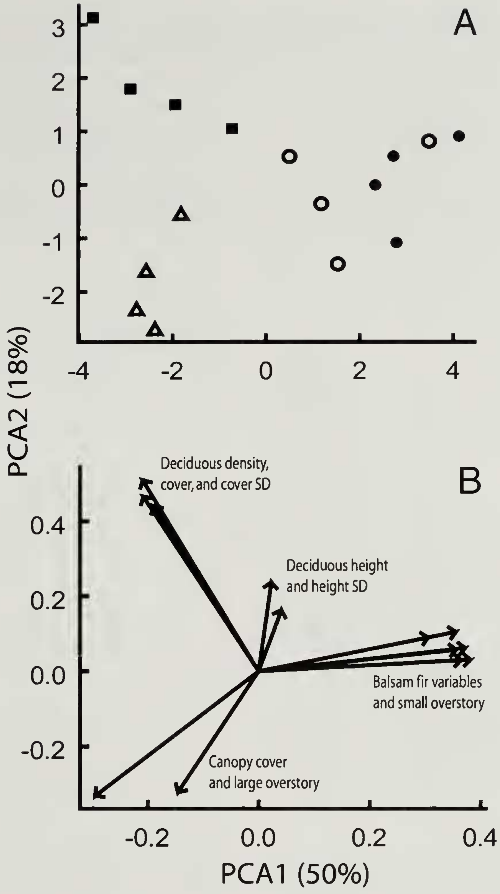

FIG. 2. Principal components analysis (PCA) showing variation in vegetation composition and structure among 36-ha plots (n = 16) in the Hiawatha National Forest, Michigan, summer 2002. (A) Plot-type distribution: triangles = minimal understory plots, squares = deciduous-dominated understory with sparse stem densities of balsam fir, open circles = understory with moderate densities of balsam fir, and closed circles = understory with high densities of balsam fir. (B) Pattern of variables along PCA axes. Axes 1 and 2 accounted for 50% and 18%, respectively, of the variation among plots. The first component positively loads balsam fir variables and the second positively loads stem density, percent cover, and patchiness of deciduous vegetation, thus separating plots containing minimal understory from deciduous-dominated understory; plots containing moderate and high stem densities of balsam fir were not clearly separated.

timation as containing moderate to high densities of balsam fir in the understory from the four minimal understory and four deciduous-dominated understory plots (Fig. 2A). Stem density of balsam fir in the understory and small-tree overstory were highly correlated (Fig. 2B). The second principle component, accounting for 18% of the variation (eigenvalue = 2.3), positively weighted deciduous understory stem density, cover, and patchiness and negatively weighted large-tree density (Table 1, Fig. 2B). This component distinguished the four minimal understory plots from the four deciduous, sparse balsam fir understory plots. The third principle component described 16% of the variation (eigenvalue = 2.0) and positively weighted deciduous understory height and vertical structure (Table 1); this component was not clearly associated with the four understory plot types.

Based on the results of the PCA, we redefined the understory categories of plots, reducing the number to three categories: minimal understory (n = 4), deciduous-dominated understory (n = 4), and balsam fir-dominated understory (n = 8). Compared to balsam fir-

TABLE 2. Mean vegetation and avian measurements (SE) for plot types after redefinition by principle components analysis: minimal understory (n = 4), deciduous-dominated understory (n = 4), and balsam fir-dominated understory (n = 8) in the Hiawatha National Forest, Michigan, summers of 2002 and 2003. Vegetation variables included measures with the largest loadings for the first three principle components and densities of overstory trees; plot types were subsequently defined by the PCA results. Deciduous- and balsam fir-dominated plots had similar total understory cover but differed with respect to composition; minimal understory plots contained more large (≥22.5 cm in diameter at breast height) trees. There were significant differences in the abundances of Black-throated Blue Warblers (BTBW) and Veerys by plot type (Kruskal-Wallis test, $P < 0.05$); between-plot differences in the ratio of older to younger male BTBWs were not significant (Kruskal-Wallis test, $P = 0.49$).

	Plot type		
Variable	Minimal understory	Deciduous-dominated understory	Balsam fir-dominated understory
Large-tree density (stems/ha)	240 (9)	162 (10)	128 (7)
Small-tree density (stems/ha)	283 (25)	306 (14)	487 (24)
Balsam fir understory			
Cover (%)	0.0 (0)	2.5 (2.5)	26.9 (2.5)
Height (m)	0.50 (0.50)	0.60 (0.35)	1.51 (0.07)
Height SD	0.09 (0.09)	0.28 (0.19)	0.83 (0.14)
Deciduous species understory			
Cover (%)	12.0 (1.9)	36.0 (5.7)	12.6 (2.1)
Height (m)	1.27 (0.14)	1.33 (0.15)	1.25 (0.10)
Height SD	0.91 (0.17)	0.98 (0.09)	0.94 (0.16)
Black-throated Blue Warbler			
Abundance (2002 banding)	0.0 (0)	3.5 (0.6)	7.1 (1.0)
Abundance (2002 point counts)	0.0 (0)	3.8 (0.9)	5.2 (0.5)
Abundance (2003 survey)	0.0 (0)	3.3 (1.0)	6.4 (1.0)
Age ratio (% older)	NA	58.8 (21.2)	77.8 (7.2)
Veery			
Abundance (2002 point counts)	1.3 (0.5)	6.5 (1.3)	4.2 (0.9)

and deciduous-dominated understories, minimal understory plots were characterized by sparse understory cover, all of which was deciduous (Table 2). Plots containing deciduous-dominated understory had a moderate amount of understory cover but sparse balsam fir understory cover (2.5% ± 2.5), whereas balsam fir-dominated plots contained moderate understory cover, of which 26.9% ± 2.5 was balsam fir (Table 2). Deciduous stems typically fell in the shortest height category: in the 12 plots with the densest understory (deciduous- and balsam fir-dominated), 66% ± 4 of the stems were 0.5–1 m tall, whereas only 15% ± 2 and 19% ± 3 fell in the 1–2 m and >2 m categories, respectively. In contrast, 40% ± 3 of the balsam firs were 0.5–1 m tall; a similar percentage were 1–2 m tall (41% ± 3), and a lower percentage (18% ± 3) fell in the >2-m height category. Finally, there were fewer large trees in the twelve plots with dense understory, and more small trees in the balsam fir-dominated plots (Table 2).

Birds.—Sixty-seven BTBWs were banded in 12 plots and 3 additional males were repeatedly observed and counted, resulting in 2–12 males per 36-ha plot. The three measures of BTBW abundance (2002 banding and point counts, and 2003 repeat surveys) were highly correlated (r = 0.90–0.92, n = 16) and the results of our analyses using each of these measures were identical. BTBW abundance differed between plot types (Kruskal-Wallis test: $k = 3$; $n_{minimal} = 4$, $n_{deciduous} = 4$, $n_{fir} = 8$; $P < 0.01$ for all three abundance measures). On average, there were 1.4 to 3.6 more BTBWs per 36 ha (low estimate: 2002 point counts; high estimate: 2002 banding data) on plots averaging 27% balsam fir understory cover than on plots with sparse balsam fir (Table 2). The positive relationship between balsam fir and BTBW abundance was apparent

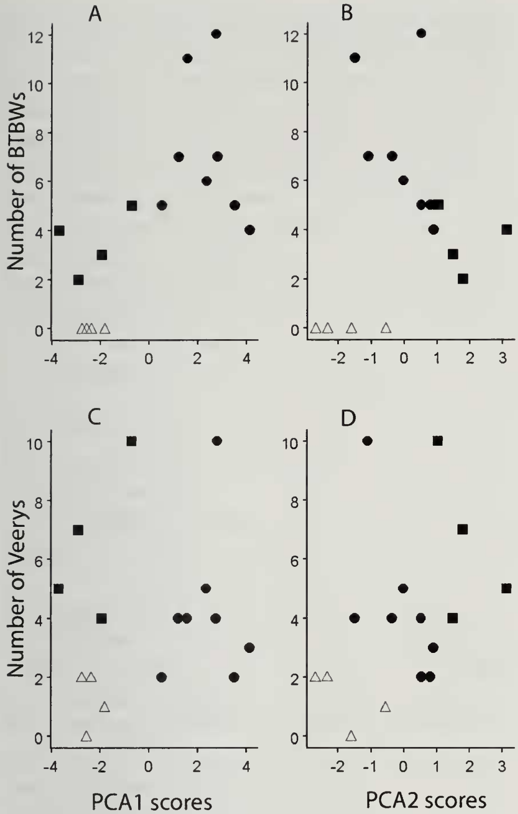

FIG. 3. Relationships between Black-throated Blue Warbler (BTBW) and Veery abundances and the scores for vegetation characteristics summarized by principal components analysis (PCA) for 36-ha plots (n = 16) in the Hiawatha National Forest, Michigan. BTBW abundance (based on banding data) in 2002 versus scores for (A) PCA 1 and (B) PCA 2; Veery relative abundance (based on point counts) in 2002 versus scores for (C) PCA 1 and (D) PCA 2. Triangles = minimal understory plots, squares = deciduous-dominated plots, and circles = balsam fir-dominated plots. For the plots that contained dense understory (n = 12), BTBW abundance increased significantly with increasing values of PCA 1 (r = 0.68), and decreased significantly with increasing PCA 2 (r = −0.65). Veery abundance was not linearly related to the PCA scores.

when BTBW abundance was compared to the first principal component (r = 0.68, n = 16, P = 0.004; Fig. 3A). Excluding plots with minimal understory, BTBW abundance showed a negative association with deciduous understory (r = −0.65, n = 12, P = 0.021; Fig. 3B). There was no relationship between BTBW abundance and the height of deciduous understory, as measured by the third principle component (r = −0.25, n = 16, P = 0.35).

Overall, 74% (52 of 70) of the BTBWs were older males in 2002. The BTBW age ratio (% older) did not differ significantly between plot types (Kruskal-Wallis test: k = 2, χ^2 = 0.47, P = 0.49; Table 2) and showed no pattern of relationship with any of the principal components (n = 12, $P > 0.25$ for all three correlations).

Veery relative abundance differed significantly by plot type (Kruskal-Wallis test: k = 3, χ^2 = 9.12, P = 0.010) and there were no significant differences among the plot types in detection probabilities by distance or time (distance: χ^2 = 3.41, P = 0.065; time: χ^2 = 2.14, P = 0.14; n = 65). Veery abundance was somewhat greater in plots with abundant deciduous understory than it was in balsam fir-dominated plots and there were few Veerys in minimal understory plots (Table 2). Veery abundance did not show any relationship to the three principle components (n = 16, $P >$ 0.20 for all three correlations; Fig. 3C, D). Thus, Veery abundance increased with understory cover, but did not show a pattern with respect to understory type (Table 2).

DISCUSSION

In maple-dominated, managed stands in the Hiawatha National Forest that experience high winter deer densities, Black-throated Blue Warbler abundance was significantly greater in areas with a dense understory of balsam fir than in areas with a dense understory of deciduous trees. Previous studies have shown that BTBWs breed in both pure stands of northern hardwoods and mixed stands of hardwood-conifer, and exhibit little preference for particular understory species if dense cover exists (Steele 1993, Holmes 1994, DeGraaf et al. 1998, Steffes 1999). In New Hampshire, BTBWs often nest in hobblebush (*Viburnum alnifolium*), a shade-tolerant deciduous shrub, probably because it is abundant and provides structural characteristics and branch heights suitable for nesting (Holway 1991, Holmes 1994). Hobblebush and shrubs with similar characteristics (e.g., *Rhododendron* spp.) used by nesting BTBW in other parts of the species' range (Holmes 1994) do not occur in most Great Lakes forests, and we suggest that at sites like ours, where most of the understory comprises regenerating tree species, balsam fir can play a role similar to that of hobblebush, particularly in areas where deer browsing reduces the abundance and heights of deciduous species. Therefore, the proportion of balsam fir in the understory, which ranged in our study from 0–40% cover in plots with 3–53% total understory cover, can be a useful tool for predicting the occurrence of BTBWs in managed, maple-dominated stands.

BTBW densities in our study area, which is near the western edge of the species' range, were low compared to those in more central parts of their range (e.g., New Hampshire, the Appalachians); this result agrees with estimates from Breeding Bird Survey data (Holmes 1994) and work by Graves (1997b). Densities averaged 0.16 ± 0.02 males/ha in plots where BTBWs were present (n = 12, maximum = 0.3), versus 0.8–0.9 males/ha in New Hampshire forest with a dense shrub layer (Holmes 1994). The presence of balsam fir and some short (<1 m) deciduous understory (presumably present due to snow protection) appears to allow BTBWs, Veerys, and other understory-dependent species to persist in these heavily deer-impacted hardwood forests. For both bird species, the peak relative abundance values were similar to high values observed in Michigan forests with much less evidence of browsing by deer (Hall 2002). Our results indicate that if local forest managers rely on studies of how deer impact bird habitats in other regions, especially those with hardwood-dominated understory (e.g., deCalesta 1994, McShea and Rappole 2000), they will underestimate habitat values for understory-dependent species at sites similar to ours.

On balsam fir-dominated understory plots with abundant BTBWs, not only were balsam fir stem densities greater, balsam firs also were taller than other understory species (Table 2). In particular, many (41%) balsam firs were 1–2 m tall, whereas most (66%) of the understory maples were <1 m tall and only 15% were in the 1–2 m category; taller deciduous stems typically showed evidence of being repeatedly browsed (i.e., many short remnants of branches persisted along the main stem). We suggest that this difference in height distribution is likely an important driver of the positive BTBW response to balsam fir at these sites. In addition to nesting in both balsam fir and deciduous cover <1 m tall, BTBWs often nested in the lower branches of balsam firs that were 1–2 m high (LJK and KRH pers. obs.). Furthermore, habitats providing a greater proportion of taller, more structurally complex saplings may provide more cover and foraging substrate for recently fledged young and adult BTBWs (Kolozsvary 2002; LJK, KRH pers. obs.) Although height differences in deciduous understory explained a substantial percentage of the vegetation variability in our study area (Table 1), this was not the focus of our sampling design. Typically, height of deciduous understory is strongly linked to both the intensity of deer browsing and time since the last selection cut or forest thinning, and further research focused on height would likely improve our understanding of habitat use by BTBWs in these forests.

Holmes et al. (1996) found that areas with more understory had greater densities of BTBWs and greater proportions of older birds. The age-ratio pattern in our plots indicated that older birds preferred areas with more balsam firs; however, the ASY:SY age ratio was not significantly greater in balsam fir-dominated plots, although these plots had the greatest densities of BTBWs. In plots where we found BTBWs, 74% were older males; this is at the high end of the range (50–79%) observed by Holmes et al. (1996) in New Hampshire, and is greater than ratios reported by Graves (1997b) for birds in northern Michigan and Ontario (50–60%). It is possible that the relative scarcity of yearling birds on our study sites precluded detection of an association between age and understory characteristics. Return rates also indicated a preference for abundant balsam fir in the understory (mean return rates were 26% in balsam fir-dominated plots and 11% in deciduous-dominated plots, a non-significant difference), but these values were based on only one year of data collected during a single survey per site.

Veery abundance did not increase as balsam fir understory increased, but Veerys were more abundant in plots with dense understory than in those with minimal understory. Veerys use a broader range of nest sites than BTBWs, including on the ground, on downed branches or logs, and in understory vegetation (Moskoff 1995; KRH unpubl. data). In a study by

Heckscher (2004), Veerys generally built their nests where dense vegetation was <1.5 m tall and there was sparse vegetation between 2.5 and 3 m high; this is consistent with our observation that Veerys were more common in sites with dense understory. We observed that Veerys commonly nested in taller firs (2–4 m), indicating that an abundance of taller balsam firs may be important in some stands, but balsam fir density alone does not appear to reliably predict the relative abundance of Veerys. The fact that a few Veerys were found at sites with little understory also suggests that factors we did not measure, such as presence of coarse woody debris, may be useful predictors of Veery abundance in Great Lakes hardwood forests.

Our results indicate that stem density of balsam fir understory predicted BTBW abundance in deer-browsed forests of northern Michigan. The density of small trees, which covaried with balsam fir and total understory density (because both variables reflect time since the last thinning or selective harvest), also predicted BTBW abundance. Balsam fir is a conspicuous plant that is easily mapped and quantified from aerial photographs taken in spring, which could make it a useful, practical indicator of BTBW habitat. Managers seeking to determine the spatial and temporal pattern of harvest activities in hardwood forest (currently, harvest methods for hardwood stands in the Hiawatha National Forest focus on selection cutting) could rank sites based on the prevalence of balsam fir and then stagger the times at which sites containing high densities of balsam fir would be harvested. We recommend that small balsam firs be left in the understory when overstory trees are removed, especially in areas most impacted by deer. Ideally, these activities would be paired with avian population monitoring to verify the effectiveness of using balsam fir density as an indicator of BTBW abundance, and to identify relationships between other songbirds and this plant species.

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